On the So-called Pharyngeal Gland-cells of Earthworms.

By

J. Stephenson, D.Sc., M.B.,

Lieutenant-Colonel, Indian Medical Service; Professor of Zoology, Government College, Lahore.

With Plate 19.

Contents.

Historical.

Succeeding the buccal cavity in all earthworms is a swollen portion of the alimentary tube, the pharynx. The usual description of this portion of the tube in Lumbricus may be given in the words of Parker and Haswell (7): the "buccal cavity . . . is followed by a much larger thick-walled, rounded chamber, the pharynx. From the wall

of the pharynx there run outwards to the body-wall a number of radially arranged bundles of muscular fibres which, when they contract, draw the pharynx backwards, and at the same time dilate it."

One of the constituents of this pharyngeal thickening, not mentioned in the ordinary descriptions of the earthworm, is nevertheless a prominent feature, easily visible under the lens in the ordinary dissection, and immediately obvious, owing to its staining properties, in sections through the region where it occurs. This constituent is a cellular mass which forms soft white projecting lobules on the dorsal and lateral aspects of the pharynx; the lobules surround the muscular strands which issue from the pharynx, and in addition, the cells of the mass penetrate inwards between the interlacing muscular bundles of the thick dorsal pharyngeal wall in the direction of the lumen of the canal.

Though these cells have received some attention from previous writers, an adequate account of their nature and origin has not yet, I believe, been given.

References to previous authors are given by Vejdovsky (9, 1884), from whose account of them I quote, since the older literature is inaccessible to me. The earlier investigators—Leo, Clarke, Lankester—who saw these masses of pharyngeal cells in Lumbricus, interpreted them as glandular. Perrier described pharyngeal glands in several genera; in Pontodrilus they are said to be variously coiled tubes whose walls are composed of large cells with granular contents; in Moniligaster they pour their secretion into the pharynx by a multitude of small canals visible with the lens; Perichæta houlleti has several layers of glands which open into the interior by three pairs of orifices. Claparède refers to those cells of the pharyngeal mass which penetrate inwards between the muscular bundles as " . . . numerous polygonal cells with large round nuclei 6 μ in diameter. The import of these cells is at present not clear to me. Their similarity to ganglion-cells is not to be denied, though a connection with nerves could not be recognised.

The matter is best left undecided at present." The projecting lobules on the dorsum of the pharynx Claparède called "ganglia of the previously described pharyngeal plexus."

Vejdovsky's own account of the pharyngeal cells is not very clear, and is interpolated here and there amongst descriptions of the muscular and vascular apparatus of the pharynx, and of the occurrence and mechanism of its extrusion. Unlike Claparède, who recognised the identity of the cells of the lobules with those which penetrate inwards between the muscular strands (interpreting both as nervous), Vejdovsky considers them as distinct. Those which penetrate inwards he looks on simply as cellular elements of the cœlomic fluid, which become attached to the pharyngeal muscles as to other organs; and he makes the rather surprising statement that "had Claparède compared these cells with those suspended in the cœlomic fluid, he would certainly have recognised them as the latter." The projecting lobules, on the other hand, are interpreted as mucous glands (Schleimdrüsen); in vertical sections the glandular masses, contracting anteriorly to form long ducts, wind between the muscular bundles of the pharynx, and most probably empty their secretion into the pharyngeal cavity; these glands extend backwards far into œsophageal segments, and correspond to the septal or mucous glands of other Oligochæta. Vejdovsky also describes the ducts of the "septal glands" of Criodrilus as winding through the layer of muscular and vascular tissue on the dorsum of the pharynx, and the exceptionally large and numerous mucous glands of Dendrobæna rubida are said to consist each of a pear-shaped mass of cells with large round nuclei and containing a substance which stains deeply in picrocarmine.

Vogt and Yung (**10**, 1888) describe irregularly dispersed cells between the muscular fibres on the dorsum of the pharynx (in Lumbricus agricola). These cells have ill-defined outlines, a granular protoplasm, and a clear spherical nucleus containing a nucleolus. The authors refer to Claparède's interpretation of them as nerve cells; they

resemble, however, the unicellular glands found in a corresponding position in other animals; and though the authors had not succeeded in discovering their ducts, they thought it not impossible that they secrete the viscid substance which the worm mixes with its food.

Hesse (**6**, 1894) considers the pharyngeal cells of Oligochæta in general as belonging to the epithelial layer; in the Naididæ and Tubificidæ the ventral end of each cell is prolonged into a duct, which debouches between the lining epithelial cells of the pharyngeal cavity; the ducts of these cells are more drawn out in Lumbricus.

Beddard (**2**, 1895) does not treat of the pharyngeal gland-cells of earthworms apart from the well-known "septal glands" of Enchytræidæ, etc. The septal glands in general, and so by implication the cells under consideration, appear to him to be simply epidermic glands which have been invaginated along with the stomodæum, though their position causes him some doubt.

The author who has examined these cellular aggregates in detail in the largest number of species, and who has given the most precise accounts of their supposed ductules and manner of discharge is Eisen (**4**, **5**, 1895, 1896). In Phœnicodrilus taste the masses (called "salivary glands") discharge through ducts which follow the muscle strands into the pharyngeal cavity; and it is probable that all the suprapharyngeal glands in Lumbricids open similarly and without any great variation as to detail; narrow ducts penetrate the pharyngeal epithelium, forming near the free surface small ovoid pockets for temporarily storing a small amount of the salivary secretion. These (suprapharyngeal) glands are connected posteriorly with the septal glands,—four pairs, superposed on several main longitudinal muscular bands which connect the pharyngeal glands with the body-wall in segment IX; their ducts, both wide and narrow, follow these muscles, so that the secretion of the septal glands also is emptied into the pharynx. In Pontodrilus michaelseni the pharyngeal or salivary glands have a similar position,

and are directly connected by means of ducts with the epithelium of the pharynx; arrived at the pharyngeal epithelium the ducts branch out, sending numerous discharge tubes between the epithelial cells; these ductules are frequently, though not generally, branched while in the epithelial layer, and each ductule is furnished at the distal end with a small storage chamber of oblong form and considerably smaller than the nucleus of the epithelial cells. There are also in this species five pairs of septal glands, ventral to the œsophagus, and principally attached to blood-vessels, in segments V–IX, of similar structure; a very thin duct runs backwards and upwards from the upper end of each towards the alimentary canal at its junction with the septum, "but I have some doubt about it emptying into the intestine, and it is much more probable that . . . these septal glands empty into the pharynx. None of my sections however show this to be the case." The distribution of the septal glands in this species may be compared with what is found in Helodrilus (Bimastus) parvus (v. p. 23 post.).

In Benhamia nana Eisen states that the glands are evidently unicellular, and the fine ducts penetrate between the epithelial cells of the pharynx, the discharge pockets being almost globular; here and there the duct of a single glandular cell may be followed clear to the discharge pocket. "But to draw the conclusion . . . that all the pharyngeal and septal glands are unicellular is, I think, premature. In Pontodrilus, at least, there may be seen plainly numerous nuclei on the gland ducts, which of course indicates that we have here a fusion of several cells. . . . In Pontodrilus the majority, and all the large glands, consisted of several cells, the respective ducts of which finally united into one. In Benhamia I could see no such union, and the single ducts could be followed with great facility to the outlets." In Benhamia nana the septal glands, in segments IX, X, and XI, are very narrow and only one cell thick in the row. In B. palmicola the small septal glands are in IX and X, but

the author could not find that they were in any way connected with the pharyngeal system of glands.

The pharyngeal and septal glands of Aleodrilus keyesi are also described. Here it will be sufficient to call attention to the author's statements regarding the discharge of the gland-cells. The pharyngeal glands have discharge pockets which are much thicker than those seen in any other species; the septal glands are of the same nature as the pharyngeal, "but I have good reasons to believe that the glands in this species discharge into the tubular intestine. I have been able to follow the discharge duct as far as the muscular layers of the intestine, which would hardly have been the case if the ducts had continued forwards into the pharynx, as do those of the forward septal glands in many genera." In some other small aggregations of similar cells the author was unable to follow the ducts.

In Sparganophilus (which, though aquatic, belongs to the Glossoscolecidæ, and so may be considered along with the earthworms), it is noted that in one species the ducts of the septal glands with precipitated secretions can be followed along the septum down towards the intestine, but the connection with the latter, if any, was not ascertained; in another species the discharge tubes and chambers are very large, the chambers occupying more than half the width of the pharyngeal wall (the meaning is more than half the height of the pharyngeal epithelium).

De Ribaucourt (**8**, 1901), describes in a few words the deeply staining mass of cells in the Lumbricidæ: "On staining with methyl blue and iodine green one can easily establish the fact that these cells are continued as far as the epithelial layer by a fine prolongation; thus the cells may quite possibly have a secretory function." Miss Raff (**7a**, 1910), recognises the cells in the Australian Megascolecidæ, but finds no trace of a duct in connection with the "glandular mass."

I omit the literature which deals with the septal glands of the specially aquatic groups—the Microdrili—as I hope to

return to these at a later date. Nor need I refer to a number of observations on the occurrence, form, and position of the pharyngeal and septal glands of earthworms by systematic writers, since these do not deal with their intimate structure.

The cells in question, therefore, are usually considered as gland-cells belonging to the epithelial layer of the alimentary tube, and they are supposed to pour their secretion into the lumen of the tube by means of long, fine ductules prolonged from the cell-body. Claparède saw no ductules, and believed the cells on the pharynx to be nervous in nature; Vogt and Yung, who nevertheless believed the cells to be secretory, could not discover the ductules; Raff also saw no duct; Vejdovsky saw "long ducts," but not, apparently, their connection with the pharyngeal cavity; de Ribaucourt saw the continuation of the cells as far as the pharyngeal epithelium; Eisen has given detailed accounts of the ductules, of their branching in the pharyngeal epithelium, and of their discharge pockets; Perrier (according to Vejdovsky) saw the ducts with a lens, and observed their paired orifices.

According to my observations the cells in question are not of epithelial origin, and have no connection with the pharyngeal epithelium. They originate at the peripheral limit of the pharyngeal mass, and are congeneric with the peritoneum; in the adult they extend deeply into the pharyngeal mass, and there become largely transformed into connective tissue; but what their primary function is I am unable to say. It will save repetition to state here that in none of my sections, which were taken in all three planes, have I seen structures that could be interpreted as ductules.

Claparède's view of the nervous nature of the cells probably originated in their superficial resemblance to the spinal ganglion cells of higher Vertebrates; there is no resemblance to the ganglion cells of the Oligochæta. Vejdovsky's statement as to the similarity to the cœlomic corpuscles of those

of the cells which lie deep among the muscular bundles of the pharynx is frankly unintelligible to me. The authors who have seen ductules and their endings in the pharyngeal epithelium have, I believe, been misled by preconceived ideas on the nature of the cells, and by the appearances due to the transformation of the deeper cells into connective tissue.

Material and Methods.

I have investigated in detail the five common species of earthworms found in Lahore; three of these, Pheretima posthuma (L. Vaill.), P. heterochæta (Mchlsn.), and P. hawayana (Rosa), belong to a genus of Megascolecidæ; two, Helodrilus (Allolobophora) caliginosus subsp. trapezoides (Ant. Dug.), and Helodrilus (Bimastus) parvus (Eisen), to the Lumbricidæ. In addition to adult specimens, I have examined a number of younger worms of both families, and also several Lumbricid embryos in various stages, taken from the cocoons; but only one of these latter gave me additional information. I am also familiar in a general way with the cell masses as they occur in a large number of other worms, which I have sectioned from time to time in the course of systematic work on Indian Oligochæta; though as I cannot answer for the histological condition of this material (which mostly formed part of the Indian Museum collections) I have not made use of it in the present account.

The methods of fixation employed were Zenker's fluid and sublimate-acetic for the embryos and smaller worms, including the adults of Helodrilus parvus; some specimens of Pheretima were also treated by one or other of these methods. Narcotisation with chloretone and fixation by 10 per cent. formalin were employed for most of the adult specimens of Pheretima and Helodrilus caliginosus.

For staining, the most generally useful method is some degree of overstaining with Delafield's hæmatoxylin, differentiation with acid alcohol, and counterstaining with alcoholic

eosin. Dobell's modification of Heidenhain's iron-hæmatoxylin method (**3**) has also given me excellent results, and I should like to confirm what its author says regarding its value and convenience. One or other of the above methods was employed for all specimens used in descriptions of the cells. In addition, I have used Heidenhain's original chromhæmatoxylin method, which gives unsurpassed differentiation of epithelial cells (skin, pharynx, œsophagus), but in my hands has been useless for the cells of the pharyngeal mass. Van Gieson's stain, and borax-carmine followed by picroindigo-carmine, were useful in differentiating the connective tissue and in distinguishing it from the muscular fibres.

I have to thank my friend and former pupil, L. Baini Prashad, M.Sc., Alfred-Patiala Research Student of the Punjab University, for kindly giving me the embryos and some of the youngest specimens used in the investigation.

Pheretima Posthuma.

General description.—In this species, in front of septum 4/5, a soft mass extends forwards almost to the anterior end of the body, filling up the available space, and hence narrower in front where the cerebral ganglion lies across it. The posterior end, or base of the somewhat conical mass, can be separated only with difficulty from septum 4/5, against which it lies, on account of the numerous strands of muscle which issue from the mass and pass backwards through the septum. When the separation has been accomplished, the posterior part of the mass is seen to be composed of numerous micronephridial tubules; the pharynx with its associated aggregations of "gland-cells" lies in front of this.

Emerging from the dorsal and lateral surfaces of the pharyngeal mass are numerous strands and sheets of muscle which take in general an obliquely backward direction; the obliquity is less in front, where the strands are more nearly transverse in direction, and greater behind, where they are

more longitudinal. Around the bases of these strands are a number of soft whitish lobular masses; these are either one to each strand, or the lobules are fused at their bases to form a transversely extended mass enveloping the origin of several strands. The whitish lobular masses are arranged in about four transverse series, and the muscle strands emerge in a corresponding number of transverse rows. The most anterior portion of the mass is smooth, and represents the thick muscular and connective tissue wall of the pharynx itself. The condition is similar to that shown in Pl. 19, fig. 1, for P. heterochaeta, omitting the masses in segment V.

In segment V, concealing the œsophagus, there is on each side posteriorly a considerable tuft of micronephridia, and anteriorly a mass of follicles of the so-called bloodglands (cf. Beddard, **1**); these latter rest against and are connected with the posterior face of septum 4–5; they interest us here because some are found more anteriorly, embedded in the cells of the posterior portion of the pharyngeal mass.

On examining longitudinal sections through the anterior end of the worm the lobules previously mentioned are found to consist of the "pharyngeal gland-cells" of earlier authors; these cells also penetrate in for some distance between the muscular fibres, which, crossing and interlacing, form the main portion of the pharyngeal mass. The pharyngeal lumen is lined by a columnar epithelium; the ventral wall of the pharynx is thin, in contrast to the massive dorsal wall; the muscular coat is here no thicker than the layer of epithelium, and the "gland-cells" are absent.

Since these cells are certainly not glandular in the sense intended by previous writers, and since their function is not fully known, it is advisable to drop the earlier name. I propose to call them chromophil cells, because of their peculiar staining properties; which, in sections stained by hæmatoxylin, for example, render the masses immediately obvious even on a naked-eye inspection.

The Chromophil cells (Pl. 19, fig. 2).—The individual

cells are of various shapes—more or less polygonal, triangular, crescent-shaped, or altogether irregular—according to the disposition of the adjacent cells. They do not however as a rule fit closely together, and are mostly well separated by clefts from their neighbours. They are usually longer in one direction than the other; the longer diameter may measure, on an average, 17 μ; the shorter, perhaps, 10 μ. Their outlines are not definite, and they are frequently continuous at their periphery with an amorphous or fibrillar coagulum-like substance, which partly fills up the intercellular spaces, and by the intermediation of which the cells may be continuous with each other.

The nucleus is often obscured by the deeply-staining portion of the cell-body to be described. It is subspherical or shortly oval, 4·5–6 μ in its long diameter. The nucleolus is large and distinct, evenly staining, and often somewhat excentrically situated; granules of chromatin occupy the more peripheral region of the nucleus (obscured in the figure).

The cell-body may be distinguished into deeply and more lightly staining portions. The deeper staining portion is always considerable in amount, and may form almost the whole of the cell-body; no further structure can be made out in this portion; it is seldom well defined in its extent, and merges into the more lightly staining portion at its periphery. The outer portion of the cells stains more lightly, and has a granular, or sometimes apparently a reticular constitution; it has often no definite peripheral boundary, the cell having a ragged edge as if its outer portion were disintegrating; or it merges into the loose substance between and sometimes connecting the cells.

Transformation of the Cells.—These cells are typically seen, and in large numbers, dorsally and posteriorly on the pharyngeal mass; where, as a compact aggregate, they form the lobules previously described, which are penetrated by the emerging muscular bundles; near the posterior limit of the mass there is in addition an admixture of follicles of "blood-

glands." Further forwards in the pharyngeal mass, dorsal to the cavity of the pharynx, in what may be called the transition zone, the cells become sparser, and interlacing muscular fibres form the bulk of the mass. In this zone the cells are seen to change their characters as they are traced gradually forwards and inwards. They become rather smaller in size; the deeply staining matter becomes less in amount, and is aggregated in smaller masses; and the cell-body becomes continued into the now abundant fibrillar strands between the muscle fibres. Numbers of such cells can be seen, which, with still a considerable amount of deeply-staining matter, dissolve at their periphery into the fibrillar or reticular packing tissue ("Füllgewebe") between the muscle fibres (compare Pl. 19, fig. 5, from P. hawayana).

Still further inwards and nearer the pharyngeal epithelium the deeply staining matter disappears altogether, and the tissue passes into the abundant connective tissue of the deeper portion of the pharyngeal mass, which is absent from the more superficial region where the typical chromophil cells are aggregated. The nuclei, no longer obscured, become conspicuous; the nucleolus diminishes in size, and ultimately disappears; the chromatin grains are distributed more evenly through the otherwise clear nucleus. But even quite near the pharyngeal epithelium occasional cells are still met with which retain the characters of those in the more superficial parts of the mass.

In this deeper region the nuclei appear to undergo a final change by becoming smaller; maintaining the above characters, they can be traced down to a size measuring 4 μ in greatest diameter. Along with these, in the connective tissue, another type of nucleus is abundantly represented; these, about 3 μ by 2 μ, are often irregular in shape; the smallest ones stain darkly, and are almost homogeneous; some appear clearer, with a few grains of chromatin. These I believe to represent the nuclei of the original connective tissue element of the muscular dorsal wall of the pharynx. They are similar to connective tissue nuclei elsewhere, and, as will

be seen, are found numerously in young specimens, where the chromophil cells have undergone little change.

I am doubtful if it is always possible to distinguish between these smaller nuclei and the last stage of transformation of the nuclei of the chromophil cells. But, in spite of the fact that discrimination of the separate elements may be impossible in the adult, it seems necessary to attribute a double origin to the connective tissue of this region.

The Capsule.—In view of what will be said later, the relation of the cells to the peritoneum is of interest. The lobular masses are surrounded by a thin capsule,—a membrane-like expansion, with fairly numerous ovoid or flattened nuclei, which show scattered chromatin granules but no nucleolus. The membrane bridges over the clefts between adjacent cells at the surface of the mass; it is in many places distinctly differentiated from the underlying cells, staining pink with eosin, and hence sharply marked off from the chromophil cells beneath. In places the membrane may contain numbers of brown chloragogen grains; in this condition it may be still a moderately thin (3–4 μ) membrane, or it may be swollen so as to be fairly described as being composed of somewhat flattened chloragogen cells; but there are no chloragogen cells of the usual elongated type. In places the capsule is absent, and the—sometimes indefinite—limits of the chromophil cells themselves form the boundary of the mass.

Pheretima heterochæta.

General description (Pl. 19, fig. 1).—In this species the cells, as in P. posthuma, form lobular masses on the pharynx (c^1); but in addition lobules composed of chromophil cells extend backwards, dorsal to the œsophagus, into segment V (c^2, c^3), where they are altogether behind the pharyngeal region of the alimentary tube. Crossing segment V in a more or less longitudinal direction are a number of muscular bands which pass backwards from the pharyngeal mass in front; the more superficial of these (m^2)

are partly, the deeper are wholly, surrounded by the soft white masses of the cells (c^2, c^3). The "blood-glands" appear as masses of grape-like follicles in segment VI, clustering round the backward prolongations of the muscle bands; follicles also occur, as seen in sections, within the lobular aggregations of the chromophil cells, both in segment V and on the pharynx.

The Chromophil Cells (Pl. 19, figs. 3, 4). The cells resemble, on the whole, those described for P. posthuma; but those of the posterior portion of the mass are in general more definite in outline than in the previous species, and do not here dissolve into the intercellular and connecting substance to the same extent. The nucleus is again characteristic,—a spherical or shortly ovoid vesicle with large nucleolus and scattered chromatin.

Transformation of the Cells.—In the backwardly projecting lobular masses of pharyngeal cells are strands of connective tissue,—a lightly-staining substance, scarcely definitely fibrillar in structure, though with an obvious longitudinal differentiation which is manifested by the deeper staining of small streaks in the direction of the length of the strand. In these strands are contained numerous cells, of the general nature of those already described; many of these dissolve at their extremities into the substance of the strand without any demarcation; some however are distinctly outlined; the nuclei may still be perfectly distinct when most of the cytoplasm has dissolved away. Indefinite masses of deeper staining material, continuous with the substance of the strands, and without nuclei, are also seen (possibly nuclei are not present merely because of the plane in which the section happens to be taken). (Compare Pl. 19, fig. 5, from P. hawayana).

Similarly amongst the muscular fibres on the dorsum of the pharynx are strands of connective-tissue of the above type with small islets of cells. The cells are in part individually distinct, in part continuous with the connective-tissue. As the transformation of the cells proceeds, the

nuclei become smaller; the nucleoli also diminish in size; and when the deeply staining substance has altogether disappeared the nuclei (or some of them) seem to disappear also, becoming fainter and less easily distinguishable; so that ultimately tracts of connective-tissue of some little size—at least as large as several of the original cells—show no nuclei at all.

The Capsule.—The lobes are surrounded by a capsule, which consists of a thin membranous sheet with not infrequent oval nuclei. This constitutes a very definite peritoneal covering over the posteriorly projecting lobules; over the more anterior masses it is less evident. But even there it can be made out in places by means of the somewhat flattened nuclei contained within a lightly staining material, which fills up little inequalities in the surface or forms small projections. In other parts however no capsule is discoverable; the limit of the mass is the limit of the chromophil cells themselves; and, as owing to the disintegration of the periphery of the cells this is not always sharply defined, it would be easy in such places to distinguish a limiting membrane if one were present (Pl. 19, fig. 4). A definite peritoneal investment covers the muscular strands which issue from the pharyngeal mass.

Pheretima hawayana.

General description.—The condition is not unlike that of the last species (Pl. 19, fig. 1). The pharynx is covered by a soft white mass, from which muscle bands emerge. Projecting behind the pharynx, and therefore in segment V, there are on each side two lobes, one above the other. The upper lobe has a smooth surface, and three muscular bands emerge from its posterior border; the lower is larger, triangular in shape with its apex backwards, smooth for the greater part, but the posterior tapering portion consists of follicles of the "blood-glands" clustering round a muscle strand. Other strands also emerge from this lobe; and on

sectioning, follicles of the "blood-glands" are found numerously within the cellular masses, even deep amongst the chromophil cells of the dorsum of the pharynx.

The Chromophil Cells and their Transformation.—The cells which compose the main portion of the white masses on and behind the pharynx are polygonal or irregular in shape, 20–25 μ in longest measurement, sometimes separated from each other by linear spaces; such have therefore a definite outline. The nucleus, up to 6 μ in greatest diameter, is conspicuous, vesicular, with large nucleolus and numerous granules of chromatin. The cytoplasm as a whole stains deeply but not homogeneously, and the lighter staining or non-staining portions of the cells appear sometimes as relatively large areas which may resemble vacuoles. (A similar condition is shown in Pl. 19, fig. 5, which, however, is from P. heterochæta.)

Besides the cells with definite outline, a number are also visible in which the central deeply staining cytoplasm shades off into a peripheral region, less deeply staining and with a fibrillar structure; this peripheral region again in places is indistinguishable from an intercellular substance.

Passing inwards towards the pharyngeal epithelium the continuity of the cells with the connective tissue, now considerable in amount, is very evident. The connective tissue accompanies the muscular fibres in close association, its fibrillæ often running parallel with the fibres. The cells still retain some of the darkly staining substance (Pl. 19, fig. 5).

Still deeper in the pharyngeal mass there may be no stainable cytoplasm in association with the nuclei; these then lie in the connective-tissue. Such nuclei are smaller, more irregular in shape, sometimes appearing shrivelled; the nucleolus decreases in size, and may become indistinguishable from the chromatin grains. Appearances suggest that some at least of these nuclei break up and disintegrate, sometimes by dividing into two small vesicles each with a staining granule in its interior, sometimes by becoming as a whole progressively more indistinct.

The Capsule.—A peritoneal covering limits the lobes in some places. The nuclei of this membrane are rounded or slightly flattened; the membrane itself is in places a distinct pink-staining (in hæmatoxylin and eosin preparations) moderately thick expansion. In some regions, while it is still possible to speak of an investing membrane, the cells composing this latter are seen to be continuous with the chromophil cells and to have the same cytoplasmic constitution. In other places no investing membrane is present.

In the adult Pheretima therefore, the chromophil cells form lobular aggregations covering the muscular mass of the dorsum of the pharynx; and in some species they also extend backwards behind the pharynx as lobe-like masses. The cells also extend deeply inwards amongst the muscular fibres in the direction of the pharyngeal epithelium; but here they become modified, the cytoplasm being progressively converted into connective tissue. The connective tissue of this region has therefore probably a double origin. The descriptions of the peritoneal capsule suggest that it and the chromophil cells are modifications of the same tissue; where the capsule is absent, the cells lining the cœlomic cavity have become chromophil cells; where present, the cells in immediate relation to the cavity have become flattened, while those underneath have taken on the chromophil character.

Lumbricidæ.

As an example of what is seen in the dissection of one of the Lumbricidæ, it will be sufficient to describe Helodrilus caliginosus, perhaps the commonest of all earthworms; the histological appearances in this species are similar in all main features to those of Pheretima (except that there are no "blood-glands" among the chromophil cells), and they therefore need not be detailed. Instead, an account of the microscopical structure of the chromophil tissue in Helodrilus parvus will be given; this species is too small to

allow of much being seen in dissection, but examined microscopically it presents a number of interesting features which go some distance towards elucidating the origin of the cells.

The Disposition of the Cell-masses in H. caliginosus (Pl. 19, fig. 6).—The combined mass of chromophil cells is situated dorsally on the pharynx, and extends backwards as far as septum 5/6. The cellular aggregate appears as a number of white lobes amongst the muscular strands; the general arrangement is one of four transverse bands. The posterior of these transverse elevations is divided into two by a cleft in the mid-dorsal line, and forms a single rounded pillow-like mass on each side (c^4). The next is not divided, and forms a single transverse elevation across the dorsum of the pharynx (c^3). The second is divided up into a number of separate lobules (c^2), and appears therefore as a transverse row of rounded projections. The first is similar to the second (c^1).

The cellular masses extend downwards on the sides of the pharynx about as far as the lateral line or a little further; the first transverse row may be shorter.

Each lobule of the two anterior rows is associated with a muscular strand (m), the base of which it surrounds. The third, undivided elevation, has a number of muscular bands emerging in a transverse series from its posterior face. The fourth is not associated with muscular strands.

The General Relations of the Cell-masses in H. parvus (Pl. 19, fig. 7).—As seen in sections, the much lobulated pharyngeal cell-mass (c^1, c^2, c^3), situated dorsal to the pharynx, extends also behind this region, and partially surrounds the first part of the œsophagus. It thus occupies segments IV, V, and VI; the portion in segment VI is to some extent separate, being divided from the rest by septum 5/6, through which it communicates with the anterior portion by a constricted neck. In segments IV and V the mass is penetrated by a number of muscular strands.

But in this species the characteristic cells have a considerably greater extent of distribution than in the forms

previously described. Thus in segments V and VI the main mass extends downwards on each side to within a short distance of the mid-ventral line (*cv*). An aggregate of cells is present in segment VII, ventrolateral to the œsophagus on each side, in close association with the lateral œsophageal ("intestino-tegumentary") blood-vessel. Similar small aggregates occur in segments VIII and IX. Small masses of cells are present dorsally in VIII, between the wall of the œsophagus and the dorsal vessel; and, at least in one specimen more minutely examined in this connection, also dorsally on the œsophageal wall in IX, in the angle between the alimentary tube and septum 8/9; on both anterior and posterior faces of septum 9/10 below the œsophagus; ventrally in segment X in association with a blood-vessel; and on the wall of the œsophagus below the dorsal vessel at the level of septum 10/11.

The Chromophil Cells.—(Pl. 19, fig. 8).—The cells are oval or irregular in shape, a small one measuring 9 μ, a large one 18 μ in greatest length. They do not fit closely together; the interspaces are empty or contain an intercellular matter.

The nucleus is large and conspicuous, vesicular, spherical or ovoid, 4 μ — 6 μ in longest diameter, often peripherally situated, and clearer than the stained cytoplasm around it. Besides small grains of chromatin there is a large nucleolus, of different material from the chromatin grains, the central portion of a bluish tinge in alcoholic iron-hæmatoxylin preparations, the periphery darker and more opaque. This large nucleolus may be absent; and then the deeply staining chromatic granules are alone visible, of which one may be larger than the rest.

The cell-body contains masses of deeply-staining material, the remainder of the cytoplasm being more slightly coloured. The less deeply staining areas are more peripherally situated; the more densely coloured portion usually encloses the nucleus, and on the whole is more central in position; it may be prolonged in one or other direction as fibril-like strands.

The intercellular substance is not as a rule sharply

marked off from the cells; the periphery of the cell fades away into the intercellular substance, and in the measurements of the cells as given above, the reference is to the deeply staining portion only, on account of the impossibility of determining the limits of cell and intercellular matter. In amount this latter may be very considerable, and the staining portions of the cells are then comparatively widely isolated from each other. It has the character of a granular amorphous matrix, into which the bodies of the cells merge, and through which some of the fibrillar processes of the deeper staining matter are continued.

Transformation of the Cells.—The chromophil cells in this species are more completely aggregated together on and behind the pharnyx than, for example, in Pheretima posthuma; the number of the cells which penetrate inwards amongst the interlacing muscular fibres on the dorsum of the pharynx is much smaller. The chromophil cells which occur between the muscular fibres are mostly isolated, or in twos and threes; in them the densely staining matter becomes less in amount, the periphery of the cell may show a reticular structure, and the cell processes are distinctly fibrillar. At a further stage the deeply staining matter disappears; the cell elongates to form a strand, the nucleus is at one side, the pale-staining fibrillæ form a reticulum. Longer strands appear, composed apparently of several cells, since they may contain one, two, or more nuclei. The nuclear changes are similar to those previously described; the nucleolus becomes smaller, and disappears or becomes indistinguishable from the chromatin grains; the nucleus itself decreases in size, and becomes faint and difficult to distinguish; appearances here again suggest that at this stage it sometimes divides; ultimately it seems to disappear.

The Capsule.—In the adult, a peritoneal capsule is present in parts over the main mass of the cells, especially posteriorly; in other species also the posterior surface appears to be the region where a recognisable capsule is best developed. But it is absent in other parts,—perhaps in

most parts ; and then the chromophil cells themselves form the limit of the mass.

The smaller masses of chromophil cells, which occur in some abundance in this species in several segments behind the main mass, show interesting relations and give considerable help in elucidating the origin of the tissue.

Relation of Chromophil Cells to Septa.—The small masses of cells on septum 9/10 are directly in contact with the muscular fibres of the septum, taking the place of the peritoneum at the spots where they occur. At one point a still smaller aggregation appears to be essentially a slight swelling of the peritoneal covering of the septum. Again at another point a single cell of the chromophil type takes its place in the series of peritoneal cells with flattened nuclei on the septum. One of the larger aggregates is continuous through the septum with a smaller mass on the other side. The aggregates, of all sizes, are continuous with the peritoneum.

Relation to the Alimentary Canal.—The cells which lie on the alimentary wall in segment IX are situated immediately outside the muscular layer. Others are in close contact with the blood-vessels which occur external to the muscular layer on the surface of the œsophagus, and not only on the outer side of the vessels, but also between the vessels and muscular fibres of the alimentary wall. In places where the muscular layer of the wall is not visible (probably because of gaps in the arrangement of the fibres), the cells are in actual contact with the epithelium of the œsophagus. Occasional cells are found singly here and there internal to the muscular layer, in the irregular space between the muscle fibres and the base of the epithelial layer.

Relations to Blood-vessels.—The cells which are situated on the lateral œsophageal trunks are in direct apposition with the muscular or connective tissue coat of the vessels, which they surround on all sides. There is no separate peritoneal coat surrounding the vessel apart from

the chromophil cells; nor any peritoneal membrane outside the cell mass.

The appearances in Helodrilus are therefore confirmatory, in general, of the results obtained from a study of Pheretima; but in addition, the facts relating to the small masses of chromophil cells on the septa, on the blood-vessels, and on the alimentary canal allow us, more decidedly than in Pheretima, to derive them from the peritoneum,—to consider them as modifications of the peritoneal layer, with which they are continuous, or the place of which they take. The occurrence of a few cells or cell aggregates in close relation to the alimentary canal is interesting in connection with former views on the nature of the cells. But here also they are to be regarded as modified peritoneal cells, which in places come in contact with the base of the epithelial layer through a hiatus in the muscular coat, or perhaps here and there make their way inwards between the muscle fibres.

The Appearances in Young Specimens.

I turn now to the results obtained from the examination of young worms, of various ages, of both genera. In the case of the Pheretimas it is impossible to be certain of the species to which young examples belong, since the discrimination of the three species which are found in Lahore is made by means of the genital system (including especially the external sexual marks). The young Lumbricids examined belonged to the smaller species, Helodrilus parvus.

Non-sexual Pheretima.—In a Pheretima which is approaching its full size but is still without sexual marks, the condition is not markedly different from that previously described. The cells of the lobular mass are irregular in shape but definite in outline; they do not dissolve at their margins into an intercellular substance. In size, 20 μ would be the greatest length of a moderately large one. The nucleus has the same general characters as in fully-grown

specimens; the large nucleolus, always present, may measure a third to two-fifths of the long, and even a half of the short diameter of the usually ovoid nucleus. Here too the cytoplasm is not uniform, but shows darker and lighter patches, the latter sometimes almost clear and vacuole-like; the darker patches are homogeneous, more or less central, and contiguous to the nucleus.

Deeper in the pharyngeal mass (Pl. 19, fig. 9) the admixture of cells is not great. The nucleus enlarges; the cell-body, smaller, dissolves at its periphery into a reticulum of fibrillar connective tissue; or the cell-body may be absent as such, having wholly broken up into fibrils, so that one side of the nucleus is bare. Still nearer the pharyngeal epithelium the nucleolus decreases in size.

The chief features of this stage are, therefore, the integrity of the cells in the lobular masses, where they have not begun to disintegrate; and, apparently, the larger size of the nucleolus. The connective tissue change is proceeding in the cells which have penetrated inwards amongst the muscle fibres.

Pheretima of diameter 1·5 mm.—The cells in the posterior and superficial portion of the mass measure 15–25 μ, are of various shapes, and well defined in outline. The cell-body consists as before of two portions, a more lightly and a more deeply staining; the latter occurring as amorphous masses, the former having a granular structure. The granules of the lighter portion appear to be the same in substance as the deeper staining masses, only not so closely aggregated; and the deeper staining portion merges into the other by becoming looser in texture.

The passage forwards towards the pharyngeal epithelium is interesting. The cells, which posteriorly are in a compact mass with only an admixture of muscle strands, become much more scattered; the muscle fibres, now arranged in a variously interwoven felt, contain within their meshwork isolated cells; the whole texture is loose. In a few cells here and there the beginning of a connective tissue change is to

be recognised; but in general even the deepest cells retain their original characters.

The cells cease altogether some distance from the pharyngeal epithelium; in other words, they have not yet distributed themselves throughout the whole pharyngeal mass. Near the pharyngeal epithelium and between the interlacing muscle fibres are scattered nuclei belonging to the sparse connective tissue of this region. These nuclei are of various and sometimes of irregular shape, and scarcely any structure is to be made out in them; the connective tissue, reticular or amorphous, is non-staining; and there is no transition between this tissue and the chromophil cells. It represents the ordinary connective tissue of the muscle, and is comparable to the connective substance between the muscle fibres in the body-wall, or in other regions of the alimentary tube. The adult connective tissue of this region has, therefore, as previously surmised, a double origin.

For the greater part of the surface of the mass there is nothing of the nature of a capsule; the margin of the mass is the distinctive cytoplasm, coarsely granular in character, of the chromophil cells, and there is an entire absence of any superficial differentiation, or of any special covering. In places however a little pinkish-staining (in hæmatoxylin and eosin preparations) matter, of a membranous or connective tissue-like appearance, is seen on the surface; sometimes the membrane is of linear tenuity, sometimes more bulky.

Where the muscle strands leave the mass a few chromophil cells appear sometimes to have travelled a little way along the strand, and hence are seen adhering to the strand just after it has emerged from the main aggregate of the cells. While some such cells appear to be underneath the peritoneal investment of the strand, others are absolutely continuous with it; in other words, some of the peritoneal cells, instead of retaining the usual flattened form, are swollen, and contain the chromophil substance.

Pheretima of diameter 1 mm.—In a still younger stage the cells, which already have a very marked chromophil

character, are still more definitely confined to the posterior and dorsal portions of the mass. They are entirely absent from half of the thickness of the mass,—that half which is nearest to the pharyngeal epithelium.

The shape of the cells is, as before, various; the outlines are well-defined, and there is for the most part no shading off into an intercellular substance. An average measurement in the longest diameter would be 15μ; 20μ would be exceptional. The nuclei are to a considerable degree obscured; they measure $3{\cdot}5$—4μ in greatest diameter, are vesicular, shortly ovoid, with large equably staining nucleolus and scattered, sometimes mainly peripheral, chromatin grains. The nuclear characters are thus already remarkably like those of the adult. The cells are rather loosely arranged, with considerable intervals.

Here and there, in the most deeply placed cells,—those which have wandered off a little from the main mass and form the outposts of the aggregate,—there is a slight indefiniteness of boundary owing to the peripheral portion of the cell-body becoming disintegrated into granular matter. But there is no formation of connective tissue; the connective tissue of the pharyngeal mass at this stage has therefore an entirely different origin. This specimen agrees with the last described in the nature of this connective tissue of the deeper part of the mass, and of its nuclei; and also in the absence or very slight and partial development of a capsule.

Summary of Appearances in Young Pheretimas.—In successively younger specimens of Pheretima therefore:

(1) The cells are more and more confined to the superficial portion of the pharyngeal mass. This is strongly suggestive of a derivation from the peritoneum; it is the opposite of what, presumably, would happen if the cells were derived from the pharyngeal epithelium.

(2) The disintegration and the transformation of the cells into connective tissue is progressively less marked.

(3) The capsule is less differentiated; the chromophil cells, which in places even in the adult border the cœlomic cavity

without the intervention of a peritoneal layer, do so in the younger stages almost over the whole surface of the mass. In other words, the chromophil cells are not derived from a previously differentiated flattened peritoneal layer; the chromophil cells, and the flattened peritoneal cells which cover neighbouring structures, are equally specializations of the lining cells of the cœlomic cavity. The inference, drawn from the appearances in the smaller masses of cells in Helodrilus parvus, that the chromophil cells are derived from the peritoneum, requires to be understood in the above sense; the often flattened cells of the peritoneal membrane, which in the adult covers the greater portion of the mass, are derived from the superficial cells of the chromophil tissue, with which (cf. the description of P. hawayana) they may still be connected, rather than vice-versâ.

Young Helodrilus Parvus.—Two small specimens, in diameter ·7 mm. in the anterior part of the body, were examined; and several still smaller, ·5 mm. in diameter; even in some of these small specimens sexual organs, both testes and ovaries, were beginning to form. Since the appearances are merely, for the most part, confirmatory of what has gone before, a short account will be sufficient.

The chromophil cells scarcely penetrate at all into the muscular felt on the dorsum of the pharynx, and form only the lobed masses round the muscular strands which emerge. In the larger of these specimens these lobes extend backwards through segments V and VI; smaller patches of the cells are present in VII, VIII, and IX on the walls of some of the blood-vessels, on the septa, and in the angle between the septum and the alimentary tube; a few cells form a flattish layer on the ventral vessel in segment X. In the smaller specimens the lobes extend backwards, segmentally arranged, as far as segment VIII; they are as usual suspended on muscular strands passing obliquely to the parietes, and are also connected in a longitudinal series through the septa by thick strands of connective tissue, which, piercing the septa as cords, spread out somewhat in the lobed masses. The

connective tissue thus forms to a certain extent a central axis for the whole, though it is not very distinct as such in the middle of the lobes. While the appearances point, as before, unmistakably to the derivation of this connective tissue from the chromophil cells, that which sparsely penetrates between the interlacing muscular fibres of the dorsum of the pharynx has equally unmistakably another origin.

Nothing that can be called a capsule is visible; the cells form the surface of the mass. Here and there in the larger specimens, in a prolonged search, are seen a few elongated, or even flattened, nuclei on or near the surface; once a little reddish (eosin) tinted material allowed a distinction to be made between a superficial layer of tissue and the chromophil cells beneath. But practically everywhere the surface of the masses is the surface—it may be the irregular or disintegrating surface—of the chromophil cells; and where the interstices between neighbouring cells come up to the surface they are not bridged over.

These young specimens confirm in all respects what was said previously regarding the relation of the smaller masses to the septa and blood-vessels in this species. The cells appear as developments of their peritoneal covering, the place of which they take, and with which they are continuous.

The Cells in the Lumbricid Embryo.

An embryo Lumbricid, pretty certainly Helodrilus caliginosus, about 2 mm. long, taken from the cocoon, yielded interesting results. Younger embryos, of which several were investigated, showed no trace of the chromophil cells.

The embryo was examined by transverse sections. Behind the region of the as yet entirely separate and laterally situated cerebral ganglia there is situated on each side, lateral to the alimentary tube, a mass of cells which appear to be dissolving into a reticular connective tissue, and amongst which a few muscular fibres are becoming differentiated.

This tissue is in two lateral masses, there being none covering the dorsal vessel (here still double), which lies directly on the gut. The tissue does not, as a whole, come in contact with the inner surface of the parietes—i. e. it does not fill up all available space between gut and body-wall, though connections with the body-wall exist in the form of strands of reticular nucleated tissue. The masses I take to be the dorsal mass of the œsophagus in an early stage.

At one place on the left side, at the periphery of this mass, is an aggregate of a few cells which are distinguishable from the rest (Pl. 19, fig. 10). These cells, about a dozen in number in the section which shows them best, and extending only through a few sections, are mostly elongated in one direction and 12–20 μ in greatest length. The nuclei are in most of the cells somewhat obscured and difficult to see; they are spherical or ovoid, 3·5–4 μ in greatest measurement, with a spherical homogeneous nucleolus of relatively considerable size, surrounded, in the cases where it is best seen, by a clear circular space; nucleolus and clear space are rather excentrically situated. The peripheral chromatin is distributed as distinct and fairly large granules. Some nuclei have two nucleoli; in other cells two relatively small nuclei are in close apposition; but I could not discover any mitotic figures (compare the various appearances of the nuclei in Pl. 19, fig. 10). The cytoplasm stains moderately deeply, but not so deeply as the chromophil substance of the adult cells; and not quite evenly, having a granular texture which is closer and more homogeneous in some parts than others.

These cells do not help to form the slightly pinkish (eosin staining) reticulum into which the main portion of the dorso-lateral pharyngeal masses seem to be dissolving. The cells are in several cases connected together among themselves, perhaps because nuclear division goes on in advance of division of the cell-body (see the upper left-hand part of the figure). No peritoneal membrane surrounds the mass; while on the body-wall the cells lining the cœlomic cavity are cubical with

spherical nuclei, or in places already flattened with elongated nuclei.

The characters of the nucleus, and to some extent those of the cytoplasm of these cells, resemble those of the chromophil cells of the adult; and it seems probable that we have here the first appearance of the characteristic cells of the pharyngeal mass. If so, they are evidently of mesoblastic origin, and make their appearance at the periphery of the pharyngeal mass.

Function of the Cells.

Though in the light of what has gone before we may reject the usual supposition, that the cells pour a secretion into the pharynx (or œsophagus, in the case of the smaller, more posteriorly situated aggregates), it is not easy to propose another hypothesis to take its place.

That some of the chromophil cells on the dorsum of the pharynx wander deeply into the pharyngeal mass in certain species and there give rise to a fibrillar connective tissue, seems plain. But this is obviously not the main function of the cells; nor does this change occur in the smaller, more posterior aggregates.

That the main function of the cells is metabolic is, though only a vague statement, perhaps as far as we are justified in going. In this connection the following considerations may be brought forward:

(A) Independently of the connective tissue change, the cells are frequently, or usually in the adult, seen to have indefinite outlines, and their margins appear to be disintegrating. This is visible even at the surface of the mass, in the cells which border the cœlomic cavity.

(B) The linear interspaces between the cells, always a marked feature, evidently allow of the easy percolation of the body fluids throughout the whole. Add to this the fact that the peritoneal capsule is never complete, and often (and especially in young specimens) largely absent, and we have the

possibility, at least, of an extensive exchange between the cells and the body-cavity fluid.

(c) The blood supply to the pharyngeal mass is extremely rich; this is a striking feature in the dissection of any earthworm in which the vessels of the anterior end of the body happen to be engorged. Not only so, but in all the species of Pheretima examined in the present paper, as well as in certain others, there are present, within and immediately behind the pharyngeal mass, large numbers of the structures known as "blood-glands". These are spherical bodies with an afferent and efferent vessel at opposite poles, containing blood, but largely choked by a mass of blood-cells. How widely these glands are distributed is not at present known; of the many score of species of Pheretima, for example, by far the larger number have as yet only been examined from a systematic point of view. Blood-glands have been found in other genera of Megascolecidæ also—in Acanthodrilus (Beddard, **1**), in Pontodrilus (first by Perrier, cf. Eisen, **5**), in Argilophilus (= Plutellus, cf. Eisen, loc. cit.)—as well as in Sparganophilus among the Geoscolecidæ (Eisen, **5**); and they not improbably occur in other genera also, where they will be revealed by a fuller examination than has yet been made. The situation of many of the smaller aggregates of chromophil cells on the blood-vessels in Helodrilus parvus may also be recalled in this connection.

(d) That active metabolism takes place in the pharyngeal region is also indicated by the great development of the nephridial tubules, in micronephridial genera, in some of the most anterior segments. Here again we are dealing with a character which is not of systematic importance, and which has, therefore, seldom been recorded. Very noticeable bunches of nephridial tubes opening to the exterior occur at the sides of the pharynx in several species examined by Miss Raff (**7a**). Bushy tufts, sometimes of relatively very great size, and always in marked contrast to the minute scattered tubules of more posterior segments, occur at the sides of and immediately behind the pharyngeal mass in, for

example, Megascolides, Notoscolex, Megascolex, Lampito, Pheretima, Erythræodrilus, Octochætus, Eutyphœus, Eudichogaster—to mention only genera in which I have myself observed them. The nephridia of meganephric forms are not enlarged in the pharyngeal and immediately subsequent segments; why no modification of any kind occurs in them, when in other and sometimes closely related genera a great multiplication and massing together of the micronephridial tubules takes place in this region, I am unable to say.

The chromophil cells do not stain with Lugol's iodine solution; glycogen seems therefore to be absent.

Summary.

(1) The "pharyngeal gland-cells" of earthworms are not gland-cells in the usual sense, and do not communicate with the pharynx; the term "chromophil cells" is proposed for them because of their intense coloration by hæmatoxylin and similar stains. The so-called "septal glands" of earthworms are aggregations of similar cells at a more posterior level.

(2) In the chromophil cells the deeply staining matter is not equably distributed through the cell-body; the peripheral regions of the cells in general stain more lightly, and appear to be disintegrating, or merge into an intercellular substance.

(3) While most of the cells form a more or less compact aggregate on the surface of the pharyngeal mass, a number penetrate inwards towards the pharyngeal epithelium, and become progressively metamorphosed into fibrillar connective tissue.

(4) A capsule of flattened cells covering the mass, though present in part, is incomplete. The smaller masses of cells in Helodrilus parvus are frequently continuous with the peritoneal membrane, of which they appear as modifications.

(5) In Helodrilus parvus, and especially in all young earthworms, the inwandering and the connective tissue change

of the chromophil cells is less marked ; in very young specimens neither has taken place. The capsule is also more and more incomplete the younger the specimen.

(6) The cells are to be looked on as of peritoneal origin ; that is to say, they are modifications of the original lining cells of the cœlomic cavity. Hence the absence of capsule in the early stages; and hence the original limitation of the cells to the superficial portion of the pharyngeal mass.

(7) The main function of the cells is probably metabolic ; but it is at present impossible to particularise further.

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EXPLANATION OF PLATE 19.

Illustrating Prof. J. Stephenson's paper, "On the So-called Pharyngeal Gland-cells of Earthworms."

Fig. 1.—Pheretima heterochæta; dissection of anterior end. c^1, Masses of chromophil cells on pharynx; c^2, upper, and c^3, lower cellular masses in segment V, behind pharynx; *d. v.*, dorsal vessel; m^1, m^2, muscular strands emerging from masses of chromophil cells; *n*, masses of micronephridia; *ph.*, pharynx; 4/5, 5/6, the corresponding septa, the latter turned back. × 8.

Fig. 2.—Chromophil cells from the pharyngeal mass of Pheretima posthuma. × 1250.

Fig. 3.—Individual chromophil cells from Pheretima heterochæta. × 1650.

Fig. 4.—Portion of the surface of the pharyngeal mass in Pheretima heterochæta, showing the general characters of the cells, clefts between the cells, and, at this place, entire absence of capsule. The surface of the mass is below in the figure. × 1000.

Fig. 5.—Chromophil cells at some depth in the pharyngeal mass of Pheretima hawayana, undergoing transformation into connective tissue. *n*. Nuclei whose stainable cytoplasm has undergone conversion, and which are themselves becoming fainter; *m*, mass of staining material, apparently without nucleus. × ca. 1250.

Fig. 6.—Helodrilus caliginosus; dissection of anterior end c^1–c^4, Lobular masses of chromophil cells on pharynx; *m*, muscular strands emerging from the masses; 5/6, 6/7, the corresponding septa (the first few septa are absent or unrecognisable). × 6.

Fig. 7.—Helodrilus parvus, an approximately median longitudinal section. c^1, Lobular masses of chromophil cells in segment IV, on dorsum of pharynx; c^2, the same in segment V; c^3, the same in segment VI; *cv*, a portion of the latter appearing ventrally; *c. g.*, cerebral ganglion; *d*, dorsal mass of the pharynx, consisting of connective tissue and muscle strands; *œs.*, œsophagus; *ph. div.*, dorsal diverticulum of pharynx; *v. n. c.*, ventral nerve cord; 4/5, 5/6, 6/7, the corresponding septa. × 40.

Fig. 8.—Chromophil cells of Helodrilus parvus. × 1250.

Fig. 9.—Chromophil cells of non-sexual Pheretima at some depth

in the pharyngeal mass. The features are the large nucleus and the relatively small amount of cytoplasm which is undergoing fibrillar change. × 2000.

Fig. 10.—Certain cells at the periphery of the loose mass dorso-lateral to the pharynx in a Lumbricid embryo. × 1650.